

# Effects of elevated CO<sub>2</sub> concentrations on photosynthesis, dark respiration and RuBPcase activity of three species seedlings in Changbai Mountain

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**Abstract:** Two-year-old seedlings of *Pinus koraiensis*, *Pinus sylvestriformis* and *Fraxinus mandshurica* were treated in open-top chambers with elevated CO<sub>2</sub> concentrations (700  $\mu\text{L}\cdot\text{L}^{-1}$ , 500  $\mu\text{L}\cdot\text{L}^{-1}$ ) and ambient CO<sub>2</sub> concentrations (350  $\mu\text{L}\cdot\text{L}^{-1}$ ) in Changbai Mountain from June to Sept. in 1999 and 2001. The net photosynthetic rate, dark respiration rate, ribulose-1,5-bisphosphate carboxylase (RuBPcase) activity, and chlorophyll content were analyzed. The results indicated the RuBPcase activity of the three species seedlings increased at elevated CO<sub>2</sub> concentrations. The elevated CO<sub>2</sub> concentrations stimulated the net photosynthetic rates of three tree species except *P. sylvestriformis* grown under 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> concentration. The dark respiration rates of *P. koraiensis* and *P. sylvestriformis* increased under concentration of 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>, but that of *F. mandshurica* decreased under both concentrations 700  $\mu\text{L}\cdot\text{L}^{-1}$  and 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>. The seedlings of *F. mandshurica* decreased in chlorophyll contents at elevated CO<sub>2</sub> concentrations.

**Keywords:** Elevated CO<sub>2</sub>; *Pinus koraiensis*; *Pinus sylvestriformis*; *Fraxinus mandshurica*

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## Introduction

Climate changes may occur in association with rising CO<sub>2</sub> concentrations, there will be direct effects of ever-increasing concentrations of CO<sub>2</sub> on plant productivity and on carbon exchange rates between terrestrial vegetation and the atmosphere. The response of a plant to rising CO<sub>2</sub> concentration may show at the leaf level firstly, and leads to a suite of changes in physiology, growth and morphology (Carla and Stan 1994). There is not a consistent conclusion on the change of net photosynthetic rate, dark respiration rate, activity of ribulose-1,5-bisphosphate carboxylase and chlorophyll content with rising CO<sub>2</sub> concentrations. The decline of photosynthesis was accompanied by a decrease of ribulose-1,5-bisphosphate carboxylase activity under elevated CO<sub>2</sub> (Stitt and Krapp 1999). However, the enhancement of atmospheric CO<sub>2</sub> concentration increased net photosynthesis because CO<sub>2</sub> is the substrate for photosynthesis, and higher concentrations of CO<sub>2</sub> resulted in more favorable competition with O<sub>2</sub> for ribulose-1,5-bisphosphate carboxylase/oxxygenase (Bowes

1996). The early results indicated that the dark respiration increased under elevated CO<sub>2</sub> concentrations (Hrabec *et al.* 1985), while current research indicated that species had lower rates of dark respiration under elevated CO<sub>2</sub> concentrations (Idso and Kimball 1992; Bunce 1990, 1991, 1992). In China, correlative research mainly focused on the response of plants grew in the pots or controlled environments and only lasted for several days, weeks or months. These short-term experiments may mask the prediction of plant response to elevated CO<sub>2</sub> concentration based solely on limited conditions. In this study, we measured the photosynthesis, respiration, ribulose-1,5-bisphosphate carboxylase activity and chlorophyll content of three tree species which have been treated with different CO<sub>2</sub> concentrations for two growing seasons.

## Materials and methods

### Experimental materials

The experiment was conducted at the Open Research Station of Changbai Mountain Forest Ecosystems, Chinese Academy of Sciences. Two-year-old *Pinus koraiensis*, *Pinus sylvestriformis* and *Fraxinus mandshurica* seedlings were grown in open-top chambers with alloy framework of 1.2 m in length, 0.9 m in width and height covered with 3-mm thick glass. During the period of experiment every tree species accepted four different treatment conditions respectively: 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>, 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>, control chamber and open field of ambient CO<sub>2</sub> concentration (about 350  $\mu\text{L}\cdot\text{L}^{-1}$ ). From June to September in 1999 and

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2000, three tree species were treated at the same time. Elevated CO<sub>2</sub> concentrations were provided day and night for two growing seasons. In the first, second and eighth week of CO<sub>2</sub> treatment in 2000, the gas exchange, chlorophyll content and enzyme activity of three tree species were determined in parallel.

Measurement of photosynthesis and respiration was made with an LCA4 portable analyzer in an open gas exchange system. Foliages measured were mature upper foliages. The stable CO<sub>2</sub> concentration for measurement came from gas-bags in which different CO<sub>2</sub> concentrations were provided in advance.

Chlorophyll of fresh foliage was extracted in 80% acetone solution and the optical density of the extract was measured at 645 nm and 663 nm wavelength against an acetone blank. Then chlorophyll content was calculated according to the formation from Arnon (Arnon 1949).

Samples for determining the activity of RuBPCase (Wang 1985) were obtained from plants in four different treatments. Fresh foliages were collected at about 9:00 a.m. and were immersed in liquid nitrogen. RuBPCase was extracted by grinding one-gram fresh weight of foliages in an ice-cooled mortar containing 5 mL (pH 7.8) Tris-HCl, EDTA 2 mmol·L<sup>-1</sup>, 2% polyvinylpyrrolidone. Crude extracts

were collected after centrifugation at 11 000×g for 10 min at 4 °C. Assays using 0.3 mL extract were conducted at 40 °C with 0.3 mL of 0.1 mol·L<sup>-1</sup> Tris-HCl (pH 7.8), 0.2 mol·L<sup>-1</sup> MgCl<sub>2</sub>, 50 mmol·L<sup>-1</sup> DTT, 1 mmol·L<sup>-1</sup> NADH, 50 mmol·L<sup>-1</sup> ATP, 1 mmol·L<sup>-1</sup> EDTA and 0.1 mL of 0.5 mol·L<sup>-1</sup> KHCO<sub>3</sub> for 20 min, and then adding to 0.1 mL PGK and GAPDH, the initial value of optical density of mixture at 340 nm wavelength was written down. The reaction was started by adding 0.1 mL of 0.5 mmol·L<sup>-1</sup> RuBP and terminated after 5 s at 25 °C.

## Results

### *Pinus koraiensis*

The every physiological index of *Pinus koraiensis* was shown in Table 1. In the first week of CO<sub>2</sub> treatments, the net photosynthetic rate of plants grown under 500 μL·L<sup>-1</sup> CO<sub>2</sub> increased by 23% and 29.9% respectively compared to those in control chamber and on open field, and the RuBPCase activity increased by 16.3% and 28.1% respectively. The dark respiration value was less than control chamber but similar to open field. The chlorophyll content decreased.

**Table 1.** The net photosynthetic rate (Pn), dark respiration rate (Rd), RuBPCase activity and chlorophyll content (Tchl) of *Pinus koraiensis* seedlings

Conditions of treatment	Time /week	Pn /μmol·m <sup>-2</sup> ·s <sup>-1</sup>	Rd /μmol·m <sup>-2</sup> ·s <sup>-1</sup>	RuBPCase /μmol·mg <sup>-1</sup> ·Pr <sup>-1</sup> ·s <sup>-1</sup>	T chl /mg·g <sup>-1</sup> ·FW
700 μL·L <sup>-1</sup> CO <sub>2</sub>	1st	6.37±0.09	-2.61±0.29	916±45	0.615±0.025
	2nd	7.46±0.15	-3.19±0.52	1251±28	0.485±0.008
	8th	10.94±1.05	-2.53±0.45	790±17	0.909±0.008
500 μL·L <sup>-1</sup> CO <sub>2</sub>	1st	5.95±0.06	-2.32±0.04	1050±18	0.454±0.027
	2nd	11.19±0.18	-1.80±0.14	1348±15	0.560±0.032
	8th	12.22±0.10	-1.85±0.04	882±35	0.937±0.063
Control chamber	1st	4.56±0.06	-1.98±0.10	878±21	0.627±0.024
	2nd	7.46±0.03	-1.43±0.14	917±16	0.775±0.003
	8th	10.38±0.42	-1.68±0.16	894±36	1.206±0.007
Open field	1st	4.17±0.03	-2.61±0.24	754±9	0.494±0.027
	2nd	7.51±0.13	-2.35±0.40	1063±34	0.633±0.009
	8th	9.63±0.07	-1.55±0.53	823±9	0.923±0.054

The net photosynthetic rate of the plants grown at 700 μL·L<sup>-1</sup> CO<sub>2</sub> increased by 28.4% and 34.5% respectively compared with that of control chamber and open field. The dark respiration showed the same change trend as that at 500 μL·L<sup>-1</sup> CO<sub>2</sub>. Compared with plants in control chamber and on open field, the RuBPCase activity increased by 4.1% and 17.7%. The values of chlorophyll content and net photosynthetic rate were higher but the RuBPCase lower than that at 500 μL·L<sup>-1</sup> CO<sub>2</sub>.

In the second week of CO<sub>2</sub> treatments, the RuBPCase activity in 500 μL·L<sup>-1</sup> and 700 μL·L<sup>-1</sup> CO<sub>2</sub> chambers was significantly enhanced, which was consistent with net photosynthetic rate. Elevated CO<sub>2</sub> concentration increased rate of carboxylation of RuBPCase, and resulted in a higher

net photosynthetic rate. The chlorophyll content of plants at 500 μL·L<sup>-1</sup> CO<sub>2</sub> was less than that of control plants, but the degree of reduction was not obvious relative to 700 μL·L<sup>-1</sup> CO<sub>2</sub>. The dark respiration at 700 μL·L<sup>-1</sup> CO<sub>2</sub> was the highest among four treatments.

In the eighth week, the net photosynthetic rates at 500 μL·L<sup>-1</sup> and 700 μL·L<sup>-1</sup> CO<sub>2</sub> maintained higher. The difference of net photosynthetic rate and RuBPCase activity between elevated CO<sub>2</sub> and ambient CO<sub>2</sub> concentration gradually decreased. In addition, the chlorophyll content of plants grown under elevated CO<sub>2</sub> concentrations increased significantly, which may be considered as an adaptation phenomenon.

***Pinus sylvestris***

The net photosynthetic rate and RuBPcase activity of *P. sylvestris* plants grown have no significant change on open field during the whole growing season (see Table 2). The RuBPcase activity in control chamber increased with time prolonging of CO<sub>2</sub> treatment and its development trend was similar to that at 500  $\mu\text{L}\cdot\text{L}^{-1}$  and 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>. This phenomenon indicated that the environment of open-top chamber itself had some effect on the RuBPcase activity. Treatment with 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> enhanced the net

photosynthetic rate of *P. sylvestris* seedlings significantly, especially in the eighth week. But the net photosynthetic rate under 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> at the end of growing season was less than control chamber and slightly more than open field. Treatment with 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> did not simulated the photosynthesis of *P. sylvestris* seedlings in the second growing season. The dark respiration rate at 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> was the highest. The elevated CO<sub>2</sub> did not make the chlorophyll content of plant decrease.

**Table 2. The net photosynthetic rate (Pn), dark respiration rate (Rd), RuBPcase activity and chlorophyll content (Tchl) of *Pinus sylvestris* seedlings**

Conditions of treatment	Time /week	Pn / $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Rd / $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	RuBPcase / $\mu\text{mol}\cdot\text{mg}\cdot\text{Pr}^{-1}\cdot\text{s}^{-1}$	T chl / $\text{mg}\cdot\text{g}^{-1}\cdot\text{FW}$
700 $\mu\text{L}\cdot\text{L}^{-1}$ CO <sub>2</sub>	1st	14.53 $\pm$ 0.07	-3.05 $\pm$ 0.42	639 $\pm$ 19	0.700 $\pm$ 0.031
	2nd	13.38 $\pm$ 0.20	-3.78 $\pm$ 0.38	784 $\pm$ 15	0.757 $\pm$ 0.017
	8th	25.23 $\pm$ 1.18	-3.34 $\pm$ 1.14	856 $\pm$ 36	0.944 $\pm$ 0.052
500 $\mu\text{L}\cdot\text{L}^{-1}$ CO <sub>2</sub>	1st	11.1 $\pm$ 0.18	-3.62 $\pm$ 0.13	599 $\pm$ 24	0.827 $\pm$ 0.021
	2nd	7.17 $\pm$ 0.04	-2.05 $\pm$ 0.12	669 $\pm$ 17	0.562 $\pm$ 0.010
	8th	13.33 $\pm$ 0.17	-3.42 $\pm$ 0.08	917 $\pm$ 15	0.760 $\pm$ 0.020
Control chamber	1st	9.56 $\pm$ 0.22	-2.93 $\pm$ 0.25	562 $\pm$ 4	0.716 $\pm$ 0.001
	2nd	9.22 $\pm$ 0.07	-2.99 $\pm$ 0.41	704 $\pm$ 8	0.749 $\pm$ 0.012
	8th	14.48 $\pm$ 0.18	-2.72 $\pm$ 0.37	827 $\pm$ 34	0.891 $\pm$ 0.042
Open field	1st	11.57 $\pm$ 0.25	-1.95 $\pm$ 0.21	746 $\pm$ 27	0.693 $\pm$ 0.029
	2nd	9.50 $\pm$ 0.10	-3.79 $\pm$ 0.39	670 $\pm$ 34	0.735 $\pm$ 0.007
	8th	10.49 $\pm$ 0.24	-3.55 $\pm$ 0.04	724 $\pm$ 18	0.762 $\pm$ 0.023

***Fraxinus mandshurica***

The higher temperature led to the reduction of net photosynthetic rate of *Fraxinus mandshurica* seedlings at both elevated and ambient CO<sub>2</sub> concentrations in the first week of CO<sub>2</sub> treatment (Table 3). The RuBPcase activity of plants in control chamber and on open field was less than that at 500  $\mu\text{L}\cdot\text{L}^{-1}$  and 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>. Elevated CO<sub>2</sub> concentration compensated for the restrain of RuBPcase activity from high temperature. The RuBPcase activity of plants under elevated CO<sub>2</sub> concentrations, especially 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>, was markedly higher than that at ambient CO<sub>2</sub> concentration in the second and eighth week. The

RuBPcase activity of control plants changed little during the whole growing season, with suggested the enzyme was affected mainly by CO<sub>2</sub> concentration. Values of chlorophyll content at ambient CO<sub>2</sub> concentration were higher than the ones at elevated CO<sub>2</sub> concentrations. The chlorophyll contents at 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> were lower than that at 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> in the first and second week, but higher than 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> in the eighth week. The dark respiration under 500 and 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> was lower than that at ambient CO<sub>2</sub> concentration. The elevated CO<sub>2</sub> concentrations caused the increase of net photosynthetic rate and the decline of dark respiration of *F. mandshurica* seedlings during the second growing season of CO<sub>2</sub> treatment.

**Table 3. The net photosynthetic rate (Pn), dark respiration rate (Rd), RuBPcase activity and chlorophyll content (Tchl) of *Fraxinus mandshurica* seedlings**

Condition of treatment	Time /week	Pn / $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Rd / $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	RuBPcase / $\mu\text{mol}\cdot\text{mg}\cdot\text{Pr}^{-1}\cdot\text{s}^{-1}$	T chl / $\text{mg}\cdot\text{g}^{-1}\cdot\text{FW}$
700 $\mu\text{L}\cdot\text{L}^{-1}$ CO <sub>2</sub>	1	4.28 $\pm$ 0.07	-0.87 $\pm$ 0.02	1535 $\pm$ 33	1.089 $\pm$ 0.045
	2	14.11 $\pm$ 0.06	-1.30 $\pm$ 0.02	1318 $\pm$ 17	1.290 $\pm$ 0.047
	8	20.37 $\pm$ 0.26	-0.61 $\pm$ 0.06	2411 $\pm$ 40	1.554 $\pm$ 0.050
500 $\mu\text{L}\cdot\text{L}^{-1}$ CO <sub>2</sub>	1	2.26 $\pm$ 0.03	-0.44 $\pm$ 0.02	1083 $\pm$ 22	1.351 $\pm$ 0.025
	2	11.29 $\pm$ 0.07	-0.71 $\pm$ 0.04	1607 $\pm$ 13	1.328 $\pm$ 0.026
	8	20.56 $\pm$ 0.19	-0.87 $\pm$ 0.06	1643 $\pm$ 30	1.302 $\pm$ 0.014
Control chamber	1	1.48 $\pm$ 0	-1.10 $\pm$ 0.12	605 $\pm$ 33	1.365 $\pm$ 0.035
	2	12.19 $\pm$ 0.34	-2.36 $\pm$ 0.49	1260 $\pm$ 11	1.500 $\pm$ 0.044
	8	8.73 $\pm$ 0.26	-0.72 $\pm$ 0.18	946 $\pm$ 24	1.757 $\pm$ 0.012
Open field	1	1.88 $\pm$ 0.05	-0.16 $\pm$ 0.07	986 $\pm$ 41	1.222 $\pm$ 0.042
	2	10.38 $\pm$ 0.14	-2.99 $\pm$ 0.56	1360 $\pm$ 40	1.368 $\pm$ 0.030
	8	11.63 $\pm$ 0.04	-0.74 $\pm$ 0.12	1199 $\pm$ 28	1.739 $\pm$ 0.094

## Discussion

There is a relationship between photosynthetic capacity and chlorophyll content, RuBPCase activity and respiration intensity (Gong 1989; Larcher 1980). At the second growing season of CO<sub>2</sub> treatment, the chlorophyll content of *Fraxinus mandshurica* seedlings decreased significantly which was consistent with the research of others (Lin *et al.* 1999; Evan *et al.* 1985). Elevated CO<sub>2</sub> concentrations increased the dark respiration of *Pinus koraiensis* and *Pinus sylvestrisformis*, but caused the decline of dark respiration of *Fraxinus mandshurica* which has been proved in Zhang's results (Zhang 2000). Now there are two comprehensive explanations about the reduction of dark respiration caused by elevated CO<sub>2</sub> concentrations. One reason can be attributed to the decline of oxygen pressure in the guard cells, and the others may also be caused by the increase of carbon dioxide pressure (Baker *et al.* 1992; Stulen and Hertton 1993). Elevated CO<sub>2</sub> concentrations enhanced the RuBPCase activity and photosynthesis of three tree species, except the photosynthesis of *Pinus sylvestrisformis* grown under 500  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub>. Higher concentrations of CO<sub>2</sub>, as the substrate for photosynthesis, result in more favorable competition with O<sub>2</sub> for RuBPCase, meantime the activity of ribulose-1,5-bisphosphate carboxylase, the primary enzyme of the photosynthetic pathway, was enhanced with the increasing concentrations of substrate. The net photosynthetic rate increased because of the increase of CO<sub>2</sub> fixed. The synchronization enhancement between CO<sub>2</sub> uptake and RuBPCase activity indicated that the latter controlled the former (Park *et al.* 1998). Still the net photosynthetic rate was not fully dominated only by enzyme activity and also related to some environmental factors of CO<sub>2</sub> concentration, temperature and moisture and so on. Some research results showed that plants grown at elevated CO<sub>2</sub> concentrations exhibited the decline of Rubisco content and activity and photosynthetic acclimation (Bowes 1991), after elevated CO<sub>2</sub> concentrations treatment of continuous two growing seasons, the *Pinus koraiensis*, *Pinus sylvestrisformis* and *Fraxinus mandshurica* seedlings did not show that phenomena mentioned above. Photosynthetic acclimation can not be only attributed to the increase of dark respiration (Rey *et al.* 1990), because both photosynthetic rate and dark respiration rate of *Pinus sylvestrisformis* grown under 700  $\mu\text{L}\cdot\text{L}^{-1}$  CO<sub>2</sub> increased.

It is difficult to conclude the eco-physiological response of plants to elevated CO<sub>2</sub> concentrations because different tree species have different response pattern. This study does not provide all information needed for predicting forest responses to changing environment. Future research must include the combined effects of physiological and morphological adjustments to estimate the effects of rising CO<sub>2</sub> concentrations on growth and carbon flux.

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